THESIS

THE USE OF ACOUSTIC COLLARS FOR STUDYING LANDSCAPE EFFECTS ON ANIMAL BEHAVIOR

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ABSTRACT

THE USE OF ACOUSTIC COLLARS FOR STUDYING LANDSCAPE EFFECTS ON ANIMAL BEHAVIOR

Audio recordings made from free-ranging animals can be used to investigate aspects of physiology, behavior, and ecology through acoustic signal processing. On-animal acoustical monitoring applications allow continuous remote data collection, and can serve to address questions across temporal and spatial scales. We report on the design of an inexpensive collar-mounted recording device and present data on the activity budget of wild mule deer (*Odocoileus hemionus*) derived from these devices, which were applied for a two-week period. Over 3,300 hours of acoustical recordings were collected from 10 deer on their winter range in a natural gas extraction field in northwestern Colorado. Results demonstrated that acoustical monitoring is a viable and accurate method for characterizing individual time budgets and behaviors of ungulates.

This acoustical monitoring technique also provides a new approach to investigate the ways external forces affect wildlife behavior. One particularly salient activity revealed by our acoustical monitoring was periodic pausing by mule deer within bouts of mastication, which appear to be adopted for listening to environmental cues of interest. While visual forms of vigilance, such as scanning or alert behavior, have been well documented across a wide range of animal taxa, animals also employ other vigilance modalities such as auditory vigilance, by listening for the acoustic cues of predators. To better understand the ecological properties that structure this behavior, we examined how natural and anthropogenic landscape variables

influenced the amount of time that mule deer paused during mastication bouts. We found that deer paused more where concealment cover abounded, and where visual vigilance was likely to be less effective. Additionally, deer paused more often at night than they did during the day, and in areas of moderate background sound levels. Our results support the idea that pauses during mastication represent a form of auditory vigilance that is responsive to landscape variables. Furthermore, these results suggest that exploring this behavior is critical to understanding an animal's perception of risk and the costs associated with vigilance behavior.

TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION

The overwhelming focus of acoustical wildlife recording has been on intentional vocalizations, which have long been studied using directional microphones to record focal animal sounds (Kroodsma 2005). Intentional vocalizations are also the focus of emerging technologies to monitor species presence and abundance using long-term, undirected recordings (Mennill et al. 2012). However, animals produce many incidental sounds that can offer valuable information about physiological, behavioral, and ecological processes. These sounds are typically much quieter than intentional vocalizations, but high quality recordings can be obtained by recording the sounds on or in close proximity to the animal. Recordings made on the animal also offer opportunities to obtain a spatiotemporal sample of the acoustical environment the animal experiences, and investigate the animal's responses to acoustical cues. Lastly, a continuous record of a free-ranging animal's acoustical environment will provide a complete record of their vocal activity, no matter where they roam.

Alkon et al. (1989) demonstrated the value of telemetered acoustical data for capturing the unintentional sounds associated with feeding, drinking, sniffing, walking, digging, and moving in dense vegetation in Indian crested porcupines (*Hystrix indica*)(Alkon et al. 1989). Subsequent studies have demonstrated the utility of recording the incidental sounds of foraging in penned deer (Nelson et al. 2005), and in domesticated mammals (Navon et al. 2012). Although the marine environment precludes wireless telemetry, acoustical recording tags have provided unique insights into the diving ecology of marine mammals (Burgess et al. 1998, Johnson and Tyack 2003). These audio tags represent a special case of the broader development

of archival tags that sense many aspects of the host organism and its marine environment (Ropert-Coudert and Wilson 2005, Naito 2010).

Wireless telemetry of audio removes the necessity of recovering the tag, but archival recordings in the tag have several advantages. It costs much less power to store data locally than to transmit it wirelessly. Local storage can deliver much higher quality audio, with wider dynamic range. Data collection is continuous no matter how far the animal travels, removing potential limitations imposed by the communication range of the wireless system. Archival tags also eliminate the need for constant observation, and permit data to be collected continuously, even when distance, darkness, or cover obscures the animal. Moreover, tags present a logical alternative to constant observation, as the presence or approach of humans has been shown to induce both subtle physiological and overt behavioral responses in wildlife (Macarthur et al. 1982, Steen et al. 1988). One potential drawback of archival tags is the installation, requiring the animal to be captured and handled for a short period of time, which can have impacts on the animal (Delgiudice et al. 1990, Montane et al. 2002, Dickens et al. 2010).

In the present study, the primary goal was to develop on-animal acoustic collars that would allow investigation of wild mule deer (*Odocoileus hemionus*) foraging and other behaviors in relation to anthropogenic noise and spatial patterns of human disturbance. We present our design criteria and discuss their realization using a consumer audio recorder. The strengths and weaknesses of our tag are summarized to inform future tag development efforts. These tags were successfully deployed on 10 free-ranging deer. The resulting acoustic data are summarized, illustrating details of mule deer activity budgets and identifying sounds related to

physiological processes and behavioral activities. These data demonstrate the potential to provide insights into species responses to anthropogenic disturbance (Francis et al. 2009) and sources of conflict with humans (Buchholz 2007).

METHODS

Collar Design

We designed and packaged ten audio recording collars (Figure 1) for mounting on mule deer using a commercially available voice recorder (DM-420, Olympus, Center Valley, PA) powered by five lithium thionyl chloride 3.6 V AA batteries. This recorder model was selected over others because of its compact physical dimensions and low power consumption (less than 30 mA at 3 V). Although the recorder was outfitted with two internal microphones, we replaced them with one small (6mm), high-gain external microphone capsule (Type PA3-IL, supercircuits.com, Austin, TX) mounted at the base of a small horn (6.19 mm throat diameter / 17.95 mm mouth diameter / 10.7 mm high). The horn provided mechanical protection for the microphone element, improved high frequency sensitivity, and offered a moderate amount of gain (area gain 9 dB above 5526 Hz) (Fristrup and Mennitt 2012). We weatherproofed the microphone and horn package with a thin sheet of plastic, which was then covered in synthetic fur fabric for wind protection. In a controlled acoustical environment (Industrial Acoustics Company, Inc., Bronx, NY), the noise floor of the complete unit was estimated to be 26.2 dBA. We configured the recorders to capture one MP3 format audio file per day to a removable 32 GB microSDHC card (because the internal memory size of the recorder was limited to 2 GB). The bitrate was set to 192 kbps for most recorders, with two units being set to 128 kbps to assess the

tradeoff between recording quality and file size. All recorders utilized a sampling rate of 44.1 kHz.

We fashioned the collar itself out of transmission belting material. To minimize risk of injury to the deer and to ensure prompt data recovery, each collar had a timed drop-off mechanism (Lotek, Ontario, Canada) programmed to disengage three weeks after the collars were mounted on the deer. A secondary detachment point (1/4" latex tubing that degrades over time) was also instituted in case of drop-off mechanism failure. To facilitate collar recovery, ear tag transmitters (series M3600, Advanced Telemetry Systems, Isanti, MN), were attached to the collars. The audio recording collar and all associated components (including batteries, recorder, and housing) weighed approximately 280 grams and cost approximately $200 each.

Field Tests

We fitted recording collars to ten does (aged 4.5-11.5 years) that were captured using helicopter net gunning as part of an intensive radio tracking study in the Piceance Basin of northwestern Colorado (Lendrum et al. 2012). Audio recording was scheduled to begin at midnight following capture to ensure that deer had adequate time to return to home ranges and that behavioral data were collected well after physiological recovery from anesthesia. In addition to the audio recording collars, each focal deer was outfitted with a GPS collar (Model G30C, Advanced Telemetry Systems, Isanti, MN).

To corroborate behavioral observations from the acoustic collars, we performed a separate validation test on a captive mule deer at the Colorado Parks and Wildlife Foothills Wildlife Facility in Fort Collins, CO. One of the collars deployed in the field test was installed

on a captive mule deer and configured to collect continuous MP3 audio files at 128 kbps. An observer simultaneously recorded the timing and sequence of several classes of behavior (browsing, ruminating, and masticating). For the purpose of the study, we define "browsing" as active intake of forage through grazing and cropping of vegetation. We categorized the intermittent regurgitations of ingesta and eructation of gas that occur during long resting or bedded periods as "ruminating." We define "mastication" as the active and prolonged mastication of ingesta. See Figure 3 and audio recordings in supplementary material for examples of these behaviors. All protocols and procedures employed were reviewed and approved under Institutional Animal Care and Use Committee (IACUC) protocol 10-2350A.

Acoustic analysis

Audio data were converted to WAV format (44.1 kHz sample rate, 16 bit) from their original MP3 format (128 kbps or 192 kbps). Data were then broken into one-second segments (44,100 samples). Finally, FFT (n = 44,100) data points were binned into the appropriate 1/3 octave center bands to produce a 1/3 octave, 1-second Leq, which ultimately produced continuous 24 hour spectrograms (Mennitt and Fristrup 2012). Spectrograms ranged in frequency from 20 Hz to 20 kHz, with 1-second time resolution. In lieu of analyzing all 3,300 hours of data, we used a random number generator to select five days of continuous audio data from one wild deer to assess within-deer variation in time spent engaged in the specified behaviors. We then randomly selected one day of continuous audio data from each of five wild deer to test the potential of collar-mounted microphones to assess inter-individual variability in estimated time budgets.

Although much ungulate behavior can be easily distinguished by listening, these sounds can be more rapidly processed by visual review of their spectrographic signatures (Figure 2). We used a spectrogram visualization tool created by the National Park Service Natural Sounds and Night Skies Division (Lynch et al. 2011) to identify and annotate periods associated with three components of foraging behavior: browsing, masticating, and ruminating. We confirmed the accuracy of behavioral annotations by referencing paired observations and recordings from the captive-deer validation test.

RESULTS

Each of the ten recording collars released on wild deer contained between 10 and 18 complete days of audio data (recordings terminated when batteries were depleted). Collar condition after the study indicated that the collars survived the harsh winter temperatures (ranging between -12 °C and 2 °C) and intermittent precipitation encountered during the study period without physical damage. The validation study on the captive deer revealed 100% agreement between observed behaviors and those detected by later visual analysis of the spectrograms and audio playback (i.e. there were no instances of disagreement between the two datasets).

Behaviors were differentiated through listening and visual review of spectrograms. Browsing could be identified by its irregular spectral pattern and was clearly distinguishable from the more rhythmic pattern created by mastication (Figure 3). During mastication each chew was defined by a sharp vertical line in a spectrogram, which was occasionally interrupted by pauses evident as an absence of sound energy (Figure 3). Similarly, there was a characteristic

signature for respirations during prolonged resting periods, and for startle events marked by the nearly instant appearance of sound energy (Figure 3). In cases of indistinct spectrogram signatures, corresponding audio files were played back to support accurate behavioral identification.

The time spent in discernible foraging activities was relatively stable for one deer across different days as well as among single days for different deer (Figure 4). Of the three components of foraging behavior we investigated, the deer spent the least time masticating (median = 16.7% for a single deer over five days and 20.8% for five deer on a single day), a moderate amount of time browsing (median = 33.0% for a single deer over five days and 33.5% for five deer on a single day), and the most time ruminating (median = 38.4% for a single deer over five days and 38.3% for five deer on a single day; Figure 2). The remainder of time was spent engaged in a variety of other behaviors. We documented frequent pausing during mastication (defined as a 3-5 sec period of complete silence during mastication bouts). Daily number of pauses during mastication for the five deer ranged from 356 to 702 with a median of 483.

By analyzing behavioral data on a continuous (24-hour) basis, we were able to gain insight into the diel patterns of masticating, browsing, and ruminating. As shown in Figure 5, browsing and ruminating were found to be negatively correlated (Spearman rank correlation coefficient = -0.71, $p < 0.001$). As might be expected from a crepuscular animal, browsing tended to occur in the early morning and late evening hours, while the deer was less active (ruminating) during the midday hours. Furthermore, while browsing and ruminating tended to

peak at certain times of day, masticating was the most consistent behavior, in that it was observed throughout the day and night hours.

We also noted occurrences of vocalizations, grooming events, footfalls associated with movement, respirations, and startle events. The collars were sensitive enough to pick up numerous ambient environmental sounds such as bird song, coyote choruses, passing vehicles and aircraft and other anthropogenic sound sources. Incidental environmental sounds rarely masked deer produced sounds, but these incidental environmental sounds were most easily identified when the deer were inactive (i.e., quiet).

DISCUSSION

We produced a durable acoustical monitoring collar capable of continuously documenting behavioral data for wild ungulates, over unlimited geographic space. Our analysis (Figure 4) indicated the Piceance mule deer time budgets were similar to those collected in other locations using telemetry. Kie *et al.* (1991) estimated that deer spend on average 32 ± 2.2 (SE) percent of the time feeding during intermittent browsing events, and 60 ± 2.4% resting (defined as either resting and/or ruminating) per 24-hour period (Kie et al. 1991) which is equivalent to the combination of our observations of mastication and rumination. While our findings of the study deer on winter range were consistent with previous estimates achieved through observation of ruminant time budgets (Wickstrom et al. 1984, Kie et al. 1991), they provide greater detail regarding these and other behaviors, and avoided observer effects that may arise from *in situ* observations. Furthermore, by sampling over continuous 24-hour time blocks, we were able to gain insight into diel patterns that could not otherwise be obtained through intermittent

observation periods. Such data can allow investigation of climatic or environmentally related variation in diel activity.

In addition to documenting foraging and food processing, our acoustical data revealed periodic pauses during mastication. While the pauses clearly serve a physiological purpose, the pauses also appear to be used for acoustic vigilance. The functions of these pauses was established by visual assessment of captive deer, which appeared to use the pauses to swallow, expire gas, and then listen to their surroundings – as indicated by movements of their pinnae. We have not found any description of auditory surveillance activity in mule deer, perhaps because previous studies have focused on other cues, or occurred in open areas where vigilance is maintained by visual scanning. The Piceance Basin is characterized by relatively thick brush in the pinyon-juniper scrub ecozone and as such, visual scanning may be less effective, requiring the deer to rely on acoustical surveillance for predator detection. Additional investigation is needed to determine what temporal and acoustical conditions are likely to produce these periodic pauses, and the significance of this apparent acoustical surveillance.

System design considerations

Fairly recent advances in audio recording technology and the advent of inexpensive, yet expansive, digital storage capacity have paved the way for the development of on-animal acoustical sensors. The collars developed for this study were constructed from economical, commercially available parts, using few production steps. Our current design required a box with dimensions generous enough to accommodate the recorder and batteries. Although the technology does not yet exist at the price point targeted, a reduction in size allowing direct

mounting to a GPS collar would be ideal. Depending on the goals of the study, it should be noted that alternate positions of the horn should be considered. In our case, we positioned the horn towards the head of the deer to collect deer produced sound. The location we chose occasionally caused artifact sounds of fur rubbing against the microphone. The predominance of deer-created sound made our recordings sub-optimal for recording ambient noise in the ecosystem, for which orienting the horn outwards would allow better monitoring of the environment. Although we could have used both orientations simultaneously, it would have cut our storage capacity in half.

As demonstrated, acoustical collars can provide detailed insight into fine-scale behaviors (including movement, communication and foraging) as well as allow novel investigation of the influence of sound disturbances on ungulates. As shown in Table 1, behavioral data produced by acoustical collars can clarify species habitat needs and nutritional ecology (Nelson et al. 2005). This technology can also be used to study foraging behavior (including intake and efficiency) of wild or domestic animals (Laca and WallisDeVries 2000), and to parameterize activity budget data and energetic modeling on a finer scale than has been produced before. On-animal audio recording devices also have the potential to advance communication studies in vocal species and to inform stimulus-response studies on a landscape scale. Finally, for acoustic ecologists interested in the effects of noise on wildlife, this type of acoustical monitoring can provide accurate measurements of the intensity of noise stimulus presented to the individual at any given time. Recent work has shown that MP3 audio can be translated into calibrated sound pressure levels (Mennitt and Fristrup 2012).

Along with many benefits, acoustical monitoring does have limitations. While it saves vast amounts of time in field observations, it also generates large datasets, which can be daunting to process. However, numerous automatic processing software packages exist (such as Raven, XBAT, SongScope, Ishmael, and many others) to help users identify signals of interest. Even so, acoustical datasets may require concurrent observational periods to confirm proper identification of ambiguous sound signals. In addition, while on-animal tags reduce the observer effect, they also require capture for installation, which may introduce both acute and chronic stress into the behavioral study system. Despite these disadvantages, acoustical monitoring remains an inexpensive, adaptable, and accurate method for recording animal behavior. Moreover, the training data we produced with manual spectrogram annotation has the potential to inform automated detection of certain behaviors across species.

TABLES

Table 1. For each study type, the audible behaviors that could be captured by an on-animal acoustical monitoring device

Study type	**Recorded sounds (behavioral or environmental)**
Time budget	Foraging, resting, grooming, walking
Communication	Vocalizing (expressed and heard)
Reproduction	Courtship, male contests, mating, birthing
Movement	Footfalls
Nutrition	Cropping rates, masticating, ruminating
Physiology	Respiring, excreting
Phenology	Timing of initiation of specific behaviors
Acoustic ecology	Audible ambient noise
Interspecific interactions (predation events)	Predator vocalizations, chasing and killing
Impacts from human disturbance	Intensity of stimulus, reacting through startle events

FIGURES

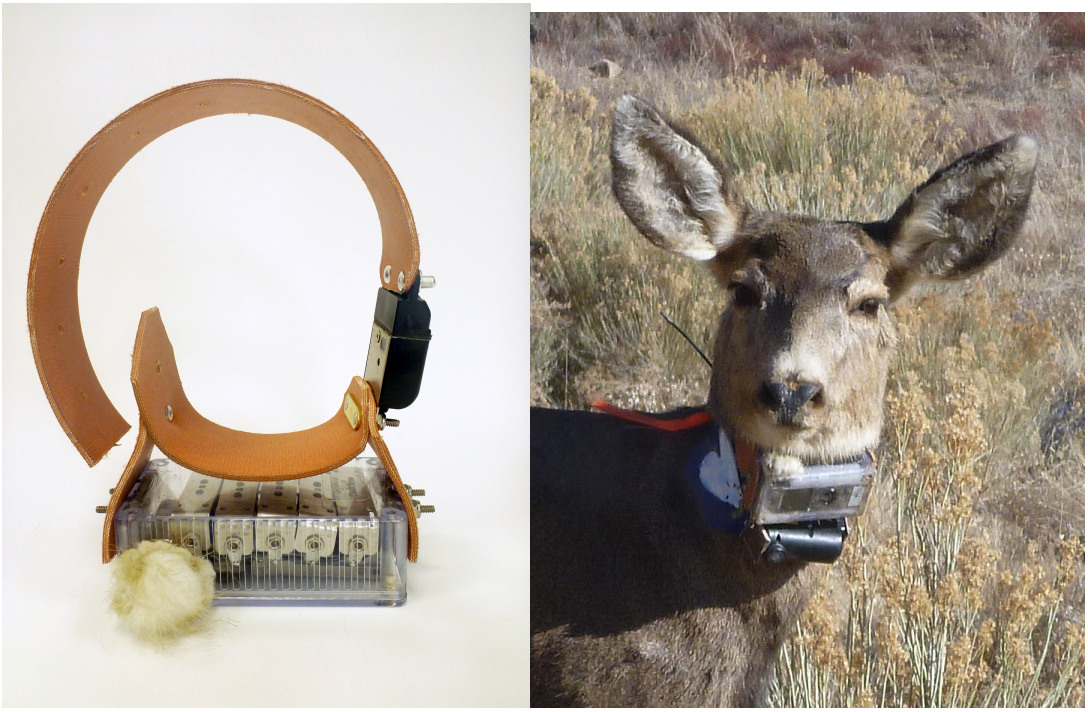

Figure 1. Photographs of acoustical monitoring collars during development (left) and implementation (right).

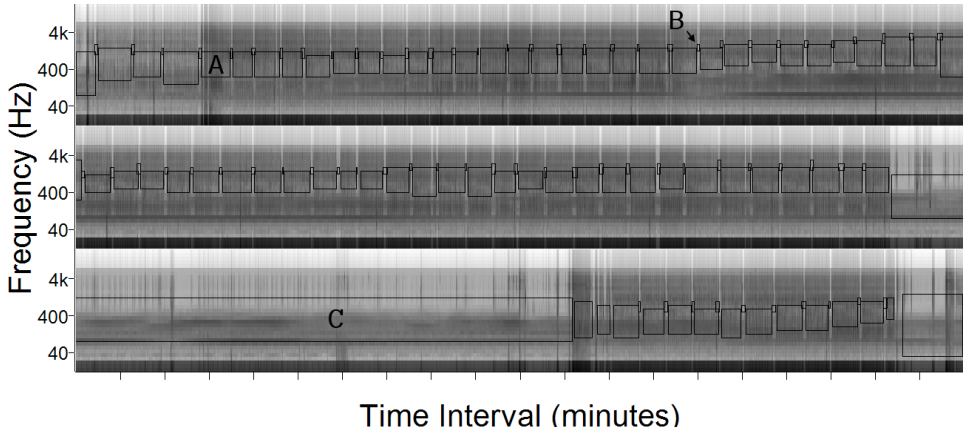

Figure 2. Spectrogram displaying one hour (1:00 – 2:00 am) of data collected from a collar-mounted recorder plotted over three 20-minute lines. The Y-axis corresponds to frequency on a logarithmic scale spanning a range of 12.5 Hz to 20 kHz. The shading scale represents intensity of sound level. Quiet background sound levels are assigned lighter shades, and sound events are assigned darker shades. The duration of distinct classes of behavior in this spectrogram have been annotated with black boxes. This hour was dominated by 75 repeated chewing events (A) that were punctuated by an equal number of pauses (B). During the long (775 second) event (C), the deer is largely inactive and likely bedded down.

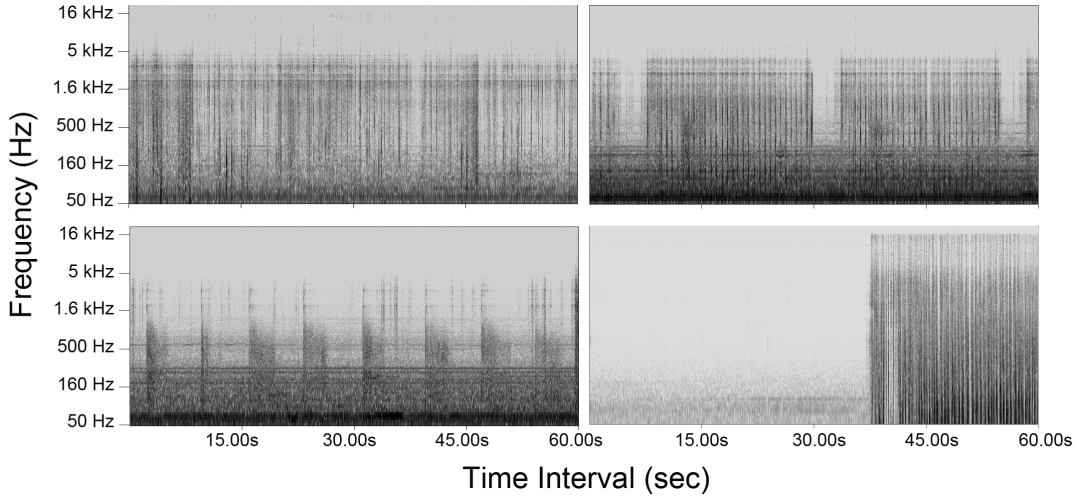

Figure 3. This figure shows four spectrograms each displaying one minute of data collected from a collar-mounted recorder. Time is displayed on the X-axis and frequency is displayed on the Y-axis on a logarithmic scale. The shading scale represents intensity of sound level. Quiet background sound levels are assigned lighter shades, and sound events are assigned darker shades. Many classes of behavior possess distinctive sound signatures. Clockwise from top left, represented behaviors are: browsing (i.e. cropping of vegetation), periodic mastication separated by three pauses, respirations (eight deep breaths) during a resting period, and a startle event initiated approximately 35 seconds into the recording.

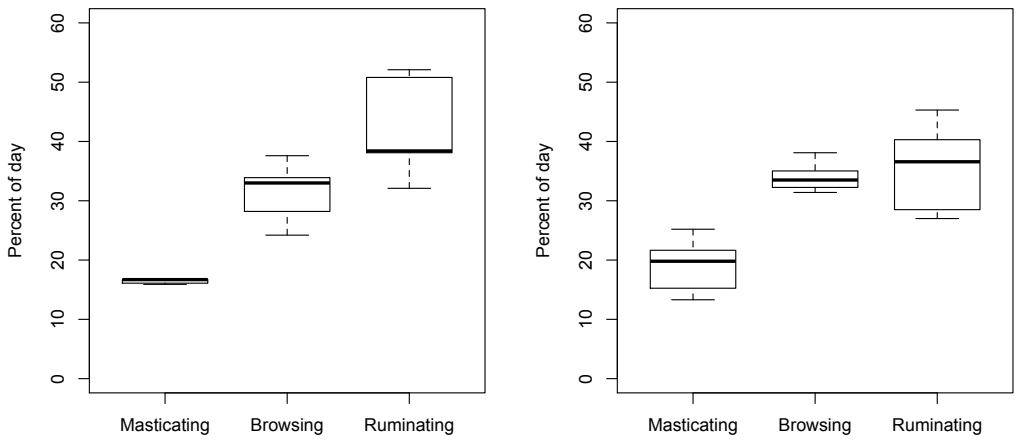

Figure 4. Median percent of day spent engaged in three components of foraging behavior measured for a single deer over multiple days (left panel; n = 5 days) and for five deer on a single day (right panel; n = 5 deer). Boxes indicate 25th and 75th percentiles, and whiskers span the range.

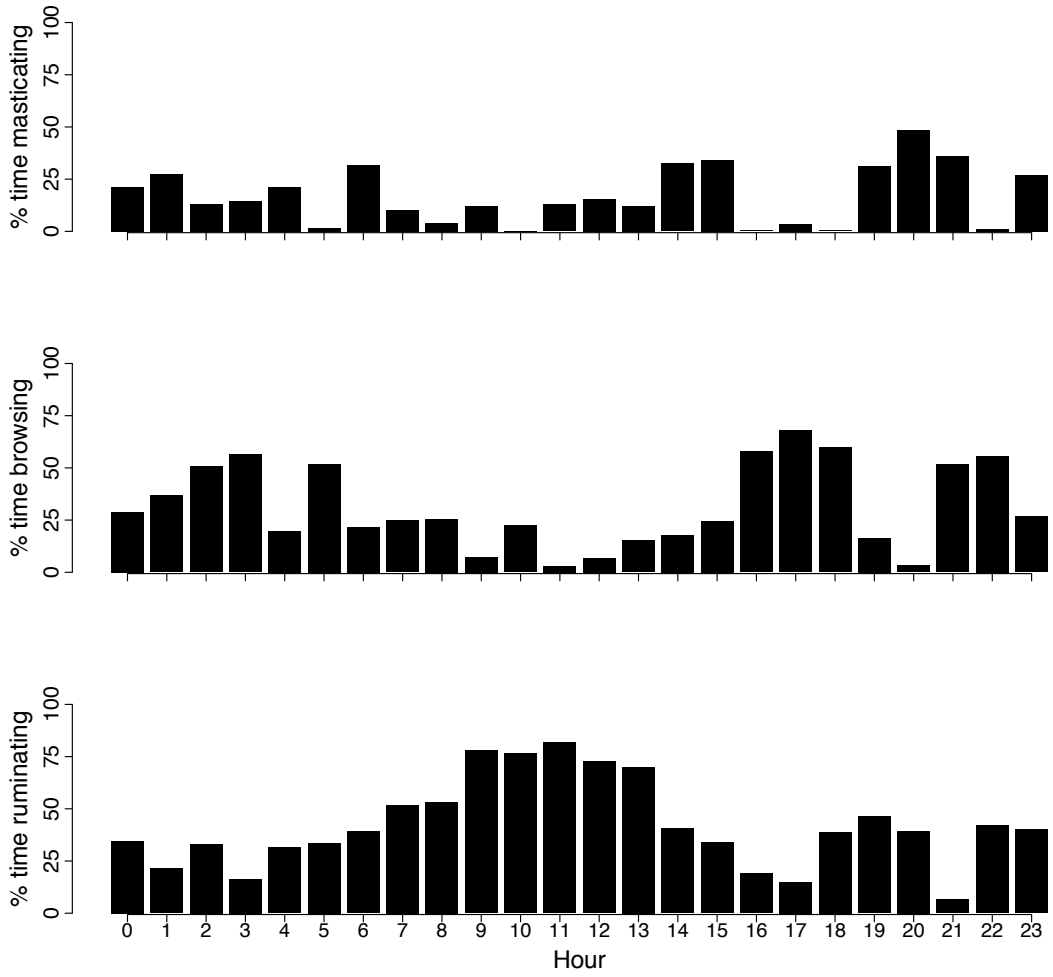

Figure 5. Mean hourly percent of time spent engaged in three behaviors (from top to bottom: masticating, browsing, and ruminating) measured for a single deer over 5 days

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CHAPTER 2

INTRODUCTION

Vigilance is an important behavioral adaptation allowing early detection and evasion of predators, thereby increasing survival (Lind 2005). Visual forms of vigilance, such as scanning or alert behavior, have been well documented across a wide range of animal taxa (Lima 1987, Quenette 1990, Frid 1997, Fortin et al. 2004). However, animals also employ other vigilance modalities such as auditory vigilance by listening for the acoustic cues of predators (Barber et al. 2010), a strategy that may be particularly valuable when environmental conditions preclude the use of sight. The time invested in vigilance is considered a tradeoff to time invested in foraging, as the act of feeding is often incompatible with predator detection (Lima and Dill 1990). Foraging is expected to detract from the visual detection of predators, and it creates incidental noise that masks acoustic cues necessary for the auditory detection of predators (Molinari-Jobin et al. 2004). Thus, prey species are expected to modulate their investment in vigilance (both visual and auditory) with varying levels of predation risk in order to maintain energy intake while also evading predation (Brown et al. 1999, Brown 1999).

Investment in antipredator behaviors such as vigilance is also expected to vary with spatial changes in perceived predation risk, often referred to as the "landscape of fear" (Brown et al. 1999, Laundré et al. 2001, Laundré et al. 2010). Major landscape factors known to influence visual forms of vigilance behavior include food density (Beauchamp 2009), distance to cover (Lima 1987), and level of human disturbance (Li et al. 2011), but the relationship between these factors is not always straightforward (Quenette 1990). Human disturbance, in particular, can have differing effects on risk perception and subsequently visual vigilance, increasing perceived

risk and vigilance when it represents a form of predation risk (Frid and Dill 2002), or reducing perceived risk when it provides a spatial refuge from predators that avoid human activity (Berger 2007, Muhly et al. 2011, Rogala et al. 2011). However, little is known about the effect of landscape variables and human disturbance on auditory vigilance, or how this behavior may interact with more commonly studied visual vigilance to structure behavioral responses to predation risk. Employment of auditory vigilance may be coupled with visual vigilance, or these behaviors may trade off in relation to characteristics that make one or the other more effective (e.g. auditory vigilance may be prevalent where landscape characteristics preclude sight). Specifically with respect to human activity, auditory vigilance may be affected in ways similar to visual vigilance, potentially increasing investment if an increase in risk is perceived; alternatively, the noise associated with human activity could reduce perceived risk by providing refuge from predators or could render auditory vigilance ineffective by masking sounds of interest, causing a decrease in its use.

To date, studies on auditory vigilance are largely absent in the literature, potentially due to the difficulty in identifying this behavior. We overcome this impediment through the use of recently developed acoustic recording collars (described in Chapter 1, Lynch et al. 2013), applying this technology to evaluate the potential role of auditory vigilance for mule deer (*Odocoileus hemionus*). A measurable indicator of effort put towards auditory vigilance is the cessation of self-noise, or pauses during bouts of noise-producing activity. Mule deer periodically pause during the mastication of ingesta, and this behavior appears to be used, at least in part, for auditory vigilance (Chapter 1, Lynch et al. 2013). In addition to serving a role in auditory surveillance, such pauses may also reflect processes unrelated to listening, including

physiological functions (e.g., the movement of ingesta, or jaw muscle relief). However, if pauses are also used for auditory vigilance, time invested in the behavior would be expected to vary with stimuli exposure and changes in landscape properties, particularly those that influence perceived levels of risk and that impede visual vigilance.

The mule deer is a prey species that is known to use vigilance as a form of antipredator behavior (Geist 1981, Altendorf et al. 2001, Lynch et al. 2013). The visual acuity of mule deer is well established, and potential dangers are often identified visually before they are close enough to be a concern (Geist 1981, Muller-Schwarze 1994, VerCauteren and Pipas 2003). However, mule deer spend up to 60 percent of their time resting (often in cover) (Kie et al. 1991), requiring the use of other keen senses such as hearing to detect approaching animals (Muller-Schwarze 1994) and other changes in the environment. In fact, both the morphology and behavior of mule deer, including their oversized pinnae that amplify sounds (Calford and Pettigrew 1984), their sensitivity to wide ranging signals (250 Hz to 30 kHz) (Geist 1981), and their ability to detect animals as far away as 600 m in any direction (using a combination of hearing and sight) (Geist 1981) suggest that acoustic signals play important roles in their sensory ecology.

We conducted this study in the Piceance Basin area of northwestern Colorado, a topographically diverse region with heterogeneous vegetative communities that is actively undergoing natural gas production and extraction. This type of development has been shown to affect behavior in a range of ungulates (Northrup and Wittemyer 2013) and elicit changes in mule deer behavior consistent with an anti-predator response (Sawyer et al. 2006) and, thus may be expected to cause an increase in their auditory vigilance. Human landscape features common

to the study area are predominantly related to energy development (i.e. roads, drilling well pads, producing well pads, and facilities such as compressors). These human landscape features produce substantial noise, potentially masking other acoustic signals, degrading the efficacy of auditory vigilance, and therefore may cause a reduction in auditory vigilance. Additionally, these disturbed areas may offer a certain level of shelter by deterring predatory species, thereby reducing perceived risk and the use of auditory vigilance. Therefore, we examine the influence of proximity to these features on auditory vigilance. We also assess the propensity for auditory vigilance in conditions known to increase the perceived predation risk of ungulates (Altendorf et al. 2001, Stankowich 2008, Laundré et al. 2010) by introducing visual barriers that inhibit visual detection of predators (Hopewell et al. 2005). Specifically, we test the predictions that auditory vigilance increases inside forested areas (relative to open regions), in rugged terrain, during nighttime hours (relative to daytime), and at closer distances to the edge of forested cover.

METHODS

Study Area

The study took place in the Piceance Basin of Northwestern Colorado, in an area that serves as winter range for mule deer from October through May. The area consists of both mixed mountain shrub and pinyon-juniper woodlands at an elevation of approximately 2,000 meters. This landscape naturally provides topographical relief and a diverse range of habitats, from dense cover to open, exposed regions (Bartmann et al. 1992). The landscape is also shaped by human activities associated with energy development, largely in the form of road networks servicing natural gas wells that are in varied phases of production or development.

Acoustic Data Collection

Ten wild mule deer, randomly selected from a multi-year global positioning system (GPS) radio tracking study (Lendrum et al. 2012, Lendrum et al. 2013) wore collar-mounted audio recording devices for approximately two weeks to track audible behaviors and ambient environmental sounds (Chapter 1, Lynch et al. 2013). Protocol and procedures employed for capture were reviewed and approved under Institutional Animal Care and Use Committee (IACUC) protocol 10-2350A. Once recovered, the recording devices provided continuous date-time stamped MPEG-2 Audio Layer III recordings. Following protocols detailed in Mennitt & Fristrup (2012), the acoustic recording collar was calibrated using a Type-1 (American National Standards Institute [ANSI] S 1.4-1983 [R 2006]) sound level meter (Larson Davis 831, Larson Davis, Depew, NY). This calibration was necessary to acquire broadband background sound levels from the collar.

Detection of Auditory Vigilance Behavior

Previous research revealed that mule deer frequently pause during mastication bouts, creating brief periods of relative quiet that could allow for auditory vigilance (Chapter 1, Lynch et al. 2013). Mastication bouts were manually identified and were defined as continuous periods of mastication, bounded by continuous periods of other behaviors such as browsing or walking. Periods of mastication and the pauses included within them were identified by examining recorded acoustic data, displayed as spectrograms with 1-second, one-third octave band resolution using the Sound Pressure Level Annotation Tool (U.S. National Park Service Natural Sounds and Night Skies Division, Fort Collins, CO). In the spectrograms, these periods were visually distinct from other behaviors (Figure 6) and were verified aurally. During these

mastication bouts, deer were typically stationary (as indicated by audio and GPS data) with their heads up, steadily processing ingesta (as indicated by audio data).

Using custom software developed in Matlab (Mathworks v. 2012b, Natick, MA), the waveforms of manually selected mastication bouts, described above, were further processed to automatically detect the start and end of pauses. The pause detector software worked on the time series data by first performing a full-wave rectification of the acoustic signal, essentially transforming the amplitude values to positive numbers. Then, the detector stepped through the data at chosen time intervals marking instances where levels dropped below a calculated percentile (described below). The dynamic threshold approach was selected because it promoted consistent detection across varying signal levels from individual collars. Pauses were then defined as the start and end periods that were consistently below the percentile threshold for a minimum duration (described below). Figure 7 displays a detected pause, marked on the original signal (A) and the rectified signal (B). The signal before and after the pause represents chewing during mastication.

To determine the appropriate time interval, percentile threshold and minimum pause duration to use in automatic detection, we evaluated the performance of 5 different combinations of values for their ability to correctly identify pauses. Correctly assigned pauses, false positives and missed pauses were identified visually within the first and last mastication bout of the two-week study period for each individual. We selected the combination of values that resulted in the lowest percentage of false positives and a high percentage of correct detections. The selected parameters were minimum pause length = 1.4 seconds, time interval = 45 seconds, and 14th

percentile threshold (Table 2), which resulted in a false positive rate of 2.025%. We applied these parameter values to all mastication bouts from all individual deer. Relevant metrics for each pause such as begin time, end time, and duration were logged (note that pauses shorter than 1.4 seconds were excluded). Moreover, a 1-second one-third octave wideband sound pressure level (SPL), extracted from the center of each pause event was used to represent the background ambient sound pressure level during the pause. In addition to the dBW wideband SPL (25 Hz – 6300 Hz), we also calculated a truncated wideband SPL (dBT) that focused on low frequency sound (20 Hz – 1250 Hz) because anthropogenic noise tends to fall on the lower end of the frequency spectrum (<2 kHz) (Francis et al. 2009, Barber et al. 2010).

Modeling natural and anthropogenic effects

To examine factors influencing variation in pause characteristics, we fit models of pause behavior in a Bayesian hierarchical framework. Our dependent variable was the proportion of the mastication bout spent paused (calculated as the sum of the duration of all pauses within a bout divided by the duration of the bout to standardize for bout length). For this variable, we fit beta regression models with intercepts varying by individual to account for the nested structure of the data (multiple bouts for each individual). Model structure is provided in Appendix A.

To extract landscape covariates for each mastication bout, we matched the time of the midpoint of each mastication bout to the GPS location for that deer that was closest in time. Deer locations were taken every 30 minutes using a GPS collar (Model G30C, Advanced Telemetry Systems, Isanti, MN). Where GPS fix failure did not make this possible, the location closest in time to the start or end of the bout was assigned to the bout if the location was taken within one hour of the bout midpoint. Bouts not associated with a successful GPS fix according to this

definition were dropped from the analysis. Consecutive bouts that occurred in spatially overlapping and temporally adjacent locations were combined into a single bout, assuming the short period of activity by the deer (e.g. brief movements and foraging) separating the bouts did not merit independent treatment. All covariates were extracted using the 'raster' package (Hijmans and van Etten 2013) in the R statistical software version 3.0.1 (R Core Team 2013).

The natural covariates (Table 3) included the distance of the deer to the edge of forested land cover (*Edge*), a binary covariate for whether it was located in forested or open land cover (*Open*), a terrain ruggedness index measuring the change in slope between the cell of interest and those surrounding it (*TR*), and a binary covariate for whether the bout occurred during the day or between sunset and sunrise (*Night*). Each of these data layers was displayed with 30 m resolution. These factors were selected because they were expected to influence perceived predation risk and the ability to detect predators visually. The anthropogenic factors (Table 3) included distance to the center of the nearest well pad with wells that were being actively drilled (*D drill*), distance to the center of the nearest well pad with only wells that were producing gas (*D prod*), distance to the center of the nearest natural gas facility (*D fac*), distance to the nearest road (*D rd*), and median wideband sound level (*dBW.med*) during the pause. These anthropogenic factors were selected because they might increase perceived predation risk (by presenting a disturbance), or they might decrease perceived predation risk (by deterring predators); further, sound levels have the potential to influence the ability to detect predators aurally. Following definitions of the Colorado Oil and Gas Conservation Commission, a well pad was considered a drilling well pad between the time that drilling began until product begins to be extracted; it was considered a producing well pad once product began to be extracted. For well

pads on which multiple wells existed, a pad was considered a drilling pad as long as at least one well was being drilled. A natural gas facility was defined as either a gas plant or compressor site.

After all covariates were extracted, we fit four separate models to the dependent variable (Table 4). All models contained all covariates described above, but the structure of each was organized to explore the functional form (linear versus non-linear) of the anthropogenic covariates. The four models were compared using deviance information criteria (DIC; Spiegelhalter et al. 2002, but as formualted by Plummer 2012), with the best fit model used to reveal which factors were significant in predicting proportion of the mastication bout spent paused. Though we calculated multiple measures of background sound level, we only report on models fit with the median dBW values because they provided a better fit (lower DIC) than models with mean dBW, mean dBT, and median dBT values (assessed separately from the four presented models). All models were fit in the R statistical software (R Core Team 2013) using the 'rjags' package (Plummer 2013; Appendix). We ran two Monte Carlo Markov chains (MCMCs) for 8,000,000 iterations, discarding the first 4,000,000 as burn-in and thinning the chains to every 10th sample. We used starting values for all parameters that were expected to be overdispersed relative to the posterior distributions and assessed convergence to the posterior distribution using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) and by examining traceplots of the MCMCs.

RESULTS

Automatic detection yielded 53,856 pause detections (an average of 5385 per individual, or 384 per individual per day over the 2 week monitoring period) during 500 mastication bouts. The median duration of a mastication bout was 1.38 hours (Interquartile Range [IQR] Lower and Upper: 0.57, 2.21). The median pause duration was 2.29 seconds (IQR: 1.79, 2.90), though a number of very long pauses (up to 6.3 seconds) were also noted in the dataset. Furthermore, a median of 3.8% (IQR: 3.4%, 4.4%) of the time spent masticating was allocated to pausing.

All models converged to the posterior distribution (Gelman-Rubin diagnostic for all parameters <1.1; Gelman and Rubin 1992). Aside from Model 4, which had quadratic terms on all distance and sound covariates (Table 4), all models had similar DIC values, indicating little difference among models (Table 4). Because it provided the best fit for the data according to DIC, we report coefficients for each covariate from Model 1 (Table 5), which were similar to and representative of the other models. As predicted, after accounting for other covariates, deer paused for a greater proportion of bouts during the night than during the day (Figure 8), and for smaller proportions of bouts when in open areas (Figure 8). Contrary to predictions, deer paused for a greater proportion of bouts when they were further from natural gas facilities (Table 5). Lastly, there was a quadratic relationship between dBW and pause behavior, whereby deer paused for a greater proportion of bouts in areas of intermediate sound level (Figure 9). The other covariates analyzed, such as distance to a road, distance to producing and drilling well pads, terrain ruggedness index and distance to the edge of forested land cover, were not significant predictors in models (<95% of posterior distribution on one side of 0)(Table 5).

DISCUSSION

Although vigilance is an important factor in ecology, the mechanisms driving the use of auditory vigilance are not well studied. This study presents one of the first detailed assessments of this potentially critical behavior. Our results indicate that pauses observed during mastication bouts were functionally applied to auditory vigilance, with variance in pausing related to landscape properties that are expected to influence perceived risk and impede visual vigilance. Consistent with predictions, we found that deer paused more extensively where concealment cover abounded and thus where visual vigilance was likely to be less effective. In addition, deer allocated a larger proportion of time to pausing during mastication bouts at night, implying that auditory vigilance is an important defense mechanism when darkness precludes visual scanning. Previous research on vigilance behavior in wild species (Lima 1987, Altendorf et al. 2001, Lind 2010) has largely overlooked the importance of auditory vigilance, potentially because this behavior is not easily seen during behavioral observations and may be obscured when it is predominantly employed, such as in association with the concealment of cover and nighttime conditions as shown here. Our results suggest that exploring this behavior is critical to understanding an animal's perception of risk and the costs associated with vigilance behavior.

It is important to note that our findings do not preclude additional explanations for pausing behavior; for example, pausing may be involved in physiological processes that may allow deer to be quiet and less likely to be detected when predators are near, or pauses may be directly induced by stimuli. As such, it is plausible that pausing during mastication serves multiple purposes simultaneously, including our supported hypothesis that variation in pausing behavior reflects shifting investment in auditory vigilance. It is notable that in our analysis, the

influence of auditory vigilance on pause duration was strong enough to overcome the confounding influence of other modalities of pausing. Our pause identification procedure excluded all pauses less than 1.4 seconds in length, effectively separating the influence of biophysical activity from the behaviorally oriented listening pauses. A more efficient procedure for separating these two pause categories would provide stronger inference regarding these behaviors and merits further investigation.

While auditory vigilance was found to increase with factors that limit the use of visual predator detection methods, we did not observe a strong response to the *Edge* or *TR* covariates. In the study area, distance from the edge of forested land cover and terrain ruggedness may not necessarily be demonstrative of visual impediment or perceived predation risk, and therefore, may not be strong predictors of auditory vigilance.

The relationship between pause duration and anthropogenic factors was complex and presented some interesting patterns. The response to background sound levels (*dBW.med^2*), which largely reflects anthropogenic sources, is demonstrative of this complexity. Higher background sound levels did not result in a greater proportion of time spent pausing. Rather, intermediate dBW values elicited the greatest response in terms of proportion of time spent pausing. This result suggests that moderate levels of background sound level elicit an increased auditory vigilance (possibly by increasing perceived predation risk), but high levels of background sound cause the behavior to decline (perhaps because it loses its utility when important auditory cues are masked) (Slabbekoorn and Ripmeester 2008, Barber et al. 2010). Additionally, extremely quiet acoustical conditions might suppress rates of auditory vigilance by

increasing the listening area (Barber et al. 2010) and reducing the need for frequent pauses. As a result, we suspect the acoustic landscape may be an important context in which to interpret responses to anthropogenic features, which tend to be associated with noise production (Barber et al. 2011).

Interestingly, deer spent a greater proportion of bouts pausing when they were further from natural gas facilities (*D fac*). Vigilance levels are expected to be higher when encounter rates with predators are perceived to be higher (Lima 1987). Therefore, a decrease in auditory vigilance in close proximity to natural gas facilities (when controlling for the influence of other covariates in the model) could imply that deer consider these areas to be less risky, possibly through predatory shielding (Berger 2007, Muhly et al. 2011). Alternatively, it is possible that deer consider natural gas facilities to be risky, but invest less in auditory vigilance in these areas because it is less effective on account of masking by noise. Lastly, it is possible that deer in this population have habituated to the noise and activity associated with natural gas development and, therefore, are not reacting to risk in the same way naïve deer might (Stankowich 2008). We did not see a strong response with respect to the distance to the drilling well covariate (*D drill*), distance to a producing well covariate (*D prod*), or distance to the nearest road covariate (*D rd*), despite the high human activity at some of these features. However we note that human activity at these features tends to be temporally dynamic, with higher activity during certain times of day or the year, potentially confounding our analysis in which these features were treated statically in time. The differences across anthropogenic features highlights the complex relationship between anthropogenic development and vigilance.

One of the negative consequences of increasing vigilance due to perceived risk is time taken away from other fitness enhancing behaviors (Frid and Dill 2002, Lind 2005). Therefore, an increase in auditory vigilance could result in a reduction in time spent foraging or, as shown here, time spent masticating, which is an important component of ungulate behavior (Wickstrom *et al.* 1984). It has been argued that vigilance can be cost-free when anti-predator vigilance is conducted during spare time (Illius and Fitzgibbon 1994), such as the interval of time between cropping and bringing a mouthful of forage fully into the mouth (Blanchard and Fritz 2007). However, unlike visual scanning, auditory vigilance cannot be conducted during the act of chewing because the sound of chewing itself masks auditory cues of interest. This trade off is emphasized in a study that reported 58 percent of roe deer were preyed upon whilst ruminating, perhaps because the act of chewing hindered the deer's ability to hear approaching predators (Molinari-Jobin et al. 2004). As such, trade-offs between noise producing behaviors and auditory vigilance may be as pertinent to animal ecology and behavior as other, more commonly studied behaviors.

In summary, auditory vigilance appears to be as salient to understanding time budgets and perceptions of risk as the more frequently studied visual vigilance behaviors. Mule deer allocated a substantial amount of time to pausing in the midst of mastication bouts during the study period, with both natural and anthropogenic landscape features differentially impacting the use of this behavior. However, further research is necessary to understand the relationship between auditory and visual vigilance behavior and how these different behaviors compliment, tradeoff, or supersede one another. Such studies might employ either simultaneous visual and auditory inspection of vigilance behavior, or accelerometry or magnetometry sensors (to gather

fine scale information about head movements and orientations) to better understand interactions between these behaviors and their landscape context. Studies assessing different contexts where these behaviors are utilized and their relative roles across other species are also needed. Finally, although the bout-level data acquired from this study did not allow us to investigate the immediate factors that influenced individual pauses, we identified a number of long pauses that closely followed significant acoustic events (such as coyote calls or vehicles passing nearby). The biologic import of these hyper-vigilant events is likely significant, and points to an exciting new approach for identifying specific predator-prey interactions.

TABLES

Table 2. Evaluation of detector performance, with parameter sets listed in the sequence tested. Bolded parameter set was selected as the best performer because it minimized false detections.

Percentile threshold	Minimum pause duration (s)	Time interval(s)	% Correct	% False	% Missed
16	0.8	30	70.393	20.921	8.686
11	0.8	30	71.914	8.587	19.499
14	**1.4**	**45**	**76.709**	**2.025**	**21.266**
12	1.1	60	78.241	5.787	15.972
12	1.1	45	78.623	6.643	14.734

Table 3. Names, descriptions, and predicted effect on proportion of bout paused for covariates used in Bayesian hierarchical models. Sources for covariates are indicated in footnotes.

Natural Covariates	**Description**	**Predicted Effect**
Edge	Distance to the edge of forested land cover[1]	-
Open	Binary covariate for being in forested land cover (0) or not (1)[1]	-
TR	Terrain ruggedness index- measure of change in slope between the cell of interest and those surrounding it[2]	+
Night	Binary covariate for whether the bout was between sunset and sunrise (1) or not (0)[3]	+
Anthropogenic Covariates		
D prod	Distance to center of producing well pad[4]	+/-
D drill	Distance to center of drilling well pad[4]	+/-
D fac	Distance to center of natural gas facility[5]	+/-
D rd	Distance to nearest road[6]	+/-
dbW.med	Median wideband sound pressure level (25 Hz - 6300 Hz)[7]	+/-

[1] Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/)
[2] Calculated from digital elevation model obtained from United States Geological Survey seamless data warehouse (http://nationalmap.gov/viewer.html)
[3] http://aa.usno.navy.mil/data/docs/RS_OneYear.php
[4] Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/)
[5] Obtained via ground truthing
[6] United States Geological Survey seamless data warehouse (http://nationalmap.gov/viewer.html) and validated through ground truthing
[7] Calculated from on-deer recording devices

Table 4. Models, model structure and deviance information criteria (DIC) values for models predicting the proportion of a mastication bout during which a deer was silent (paused).

Model	Structure	DIC
1	Edge + Open + TR + Night + log(D prod) + log(D drill) + log(D fac) + log(D rd) + dbW.med + $dbW.med^2$	-1884
2	Edge + Open + TR + Night + D prod + D drill + D fac + D rd + dbW.med + $dbW.med^2$	-1882
3	Edge + Open + TR + Night + D prod + D drill + D fac + D rd + dbW.med	-1882
4	Edge + Open + TR + Night + D prod + $D\ prod^2$ + D drill + $D\ drill^2$ + D fac + $D\ fac^2$ + D rd + $D\ rd^2$ + dbW.med + $dbW.med^2$	-1878

Table 5. Representative model (Model 1) for the proportion of bout paused with median coefficient values and 95% credible intervals (CI) for each covariate. Significance is indicated with bold font.

Covariate	Median Coefficient	95% CI	
Edge	0.035	-0.022	0.09
Open	**-0.119**	**-0.23**	**-0.009**
TR	0	-0.002	0.002
Night	**0.377**	**0.272**	**0.483**
log(D drill)	-0.009	-0.1	0.083
log(D fac)	**0.194**	**0.097**	**0.292**
log(D rds)	0.067	0.006	0.13
log(D prod)	-0.03	-0.1	0.042
dbW.med	0.079	-0.032	0.191
$dbW.med^2$	**-0.055**	**-0.104**	**-0.006**

FIGURES

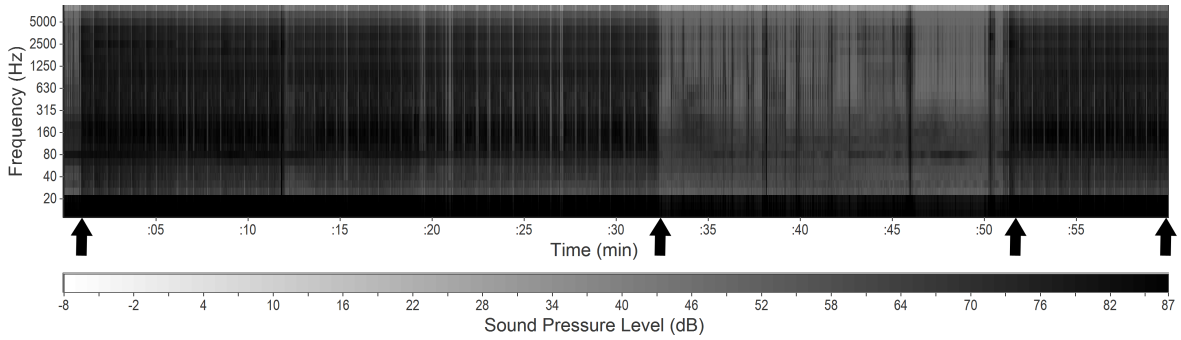

Figure 6. Hour-long spectrogram of mule deer behavior. High sound pressure levels are indicated by darker shades, low sound pressure levels are indicated by lighter shades. Two mastication bouts are distinguishable from :01 to :33 minutes, and again from :51 to :59 minutes as areas of higher sound levels (see arrows). Pauses are located within each bout, and are represented by lighter shaded vertical stripes of varying width. Between mastication bouts, the deer was stationary, intermittently inhaling, exhaling, and eructating. The dark horizontal stripe seen throughout the hour at 80 Hz corresponds to the sound of mechanized equipment (such as a generator or compressor station).

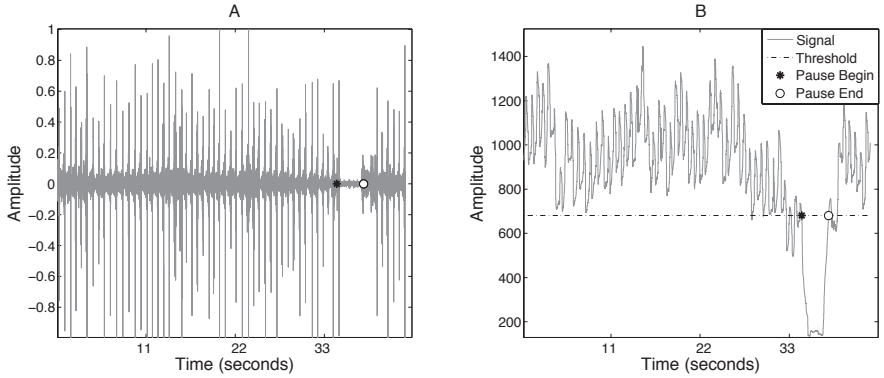

Figure 7. Example of automatic pause detection. Begin (*) and end (o) times of a single pause are marked in the original time series data (A) and on the rectified signal (B). Detection percentile threshold is marked by dotted line on the right panel. Detector was triggered to mark a pause when the signal dropped below this percentile for at least 1.4 seconds.

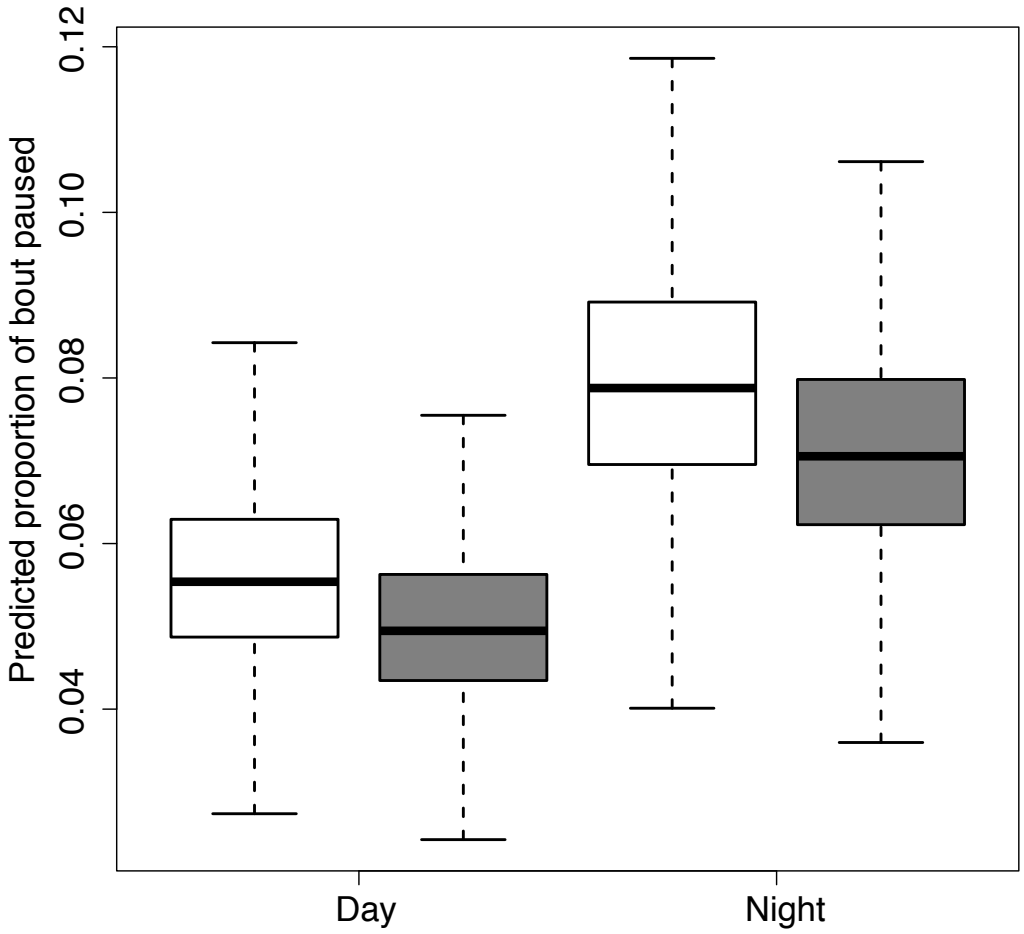

Figure 8. Predicted median and interquartile range (IQR) for predicted proportion of bout paused for day and night time periods (derived from fitted model), where predicted proportion is standardized by bout length. Dashed lines extend to 95% credible interval. Forested landcover is represented by white boxes and open areas are represented by grey boxes.

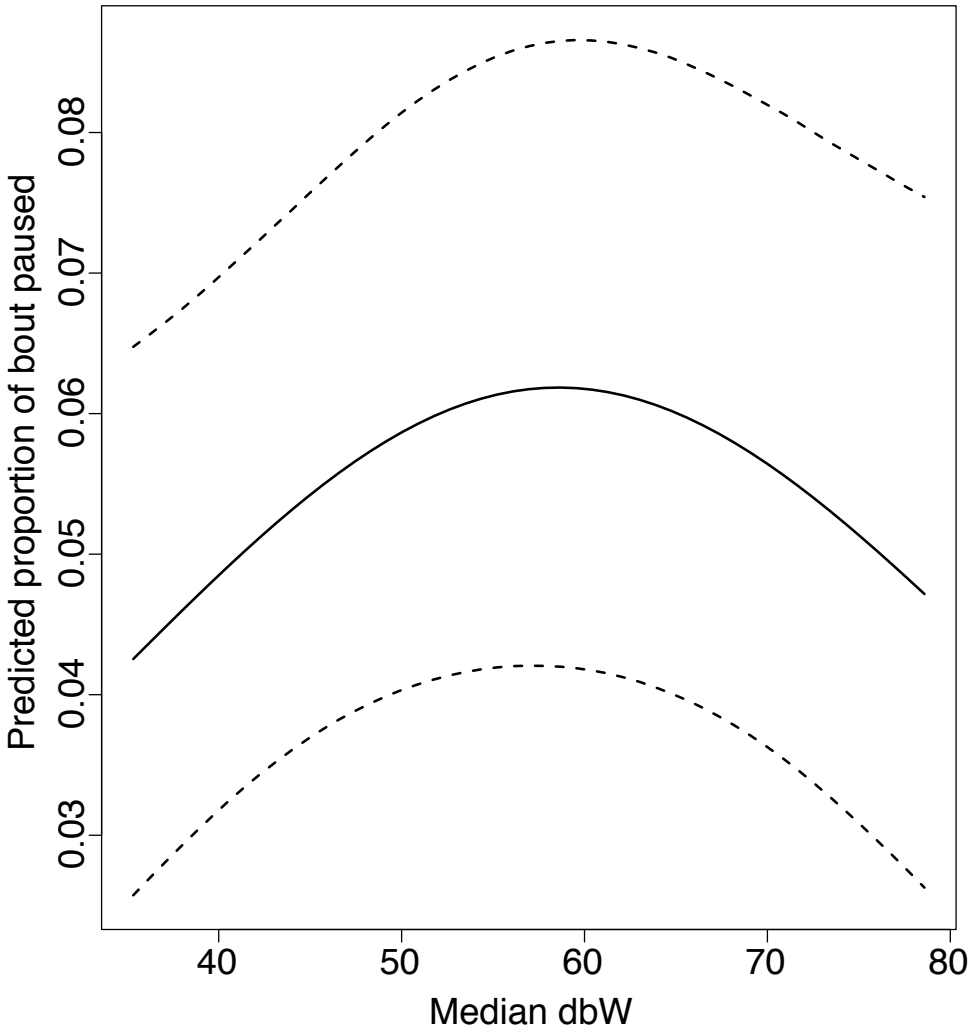

Figure 9. Predicted proportion of bout paused by median dBW (25 Hz – 6300 Hz) values (solid line) with 95% credible interval (dotted lines). Predicted proportion is standardized by bout length.

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APPENDIX A

A. Code for beta regression model (JAGS)

```
model{

#priors
mu.b0~dnorm(0,0.00001)
tau.b0~dgamma(0.001,001)
beta[1:n.beta]~dmnorm(mu.beta[], omega.beta[,])
# tau.eps~dgamma(0.001,0.001)
# sigma.eps<-1/sqrt(tau.eps)
r~dunif(0,100)

#individual intercepts
for(j in 1:n.indiv){
b0[j]~dnorm(mu.b0, tau.b0)
 }

#model
for(i in 1:length(y)){
log(lambda[i])<-b0[indiv[i]] + beta[1]*x1[i] + beta[2]*x2[i] + beta[3]*x3[i] + beta[4]*x4[i] +
offset[i]
p[i]<-r/(r+lambda[i])
y[i]~dnegbin(p[i],r)
}
}
```

B. Model outputs

Pause duration
Model 1

Covariate	Median Coeff.	Prob -	Prob +
Edge	0.022243	0.257419	0.742581
Open	-0.13082	0.970566	0.029434
D prod	-0.07797	0.92232	0.07768
D prod^2	0.045018	0.063904	0.936096
D drill	-0.00422	0.521774	0.478226
D drill^2	0.058304	0.159119	0.840881
D fac	0.251687	0.000511	0.999489
D fac^2	0.046768	0.141828	0.858173
TR	0.000683	0.28986	0.71014
D rd	0.041298	0.21755	0.78245
D rd^2	-0.01139	0.680654	0.319346
dbW.med	0.034512	0.307808	0.692193
dbW.med^2	-0.0333	0.85824	0.14176
Night	0.379152	0	1

Model 2	Median Coeff.	Prob -	Prob +
Edge	0.034631	0.151781	0.848219
Open	-0.11933	0.962809	0.037191
log(D prod)	-0.02959	0.75582	0.24418
log(D drill)	-0.00886	0.564614	0.435386
log(D fac)	0.19435	0.000458	0.999543
TR	0.000452	0.355923	0.644078
log(D rd)	0.067082	0.035625	0.964375
dbW.med	0.078662	0.123956	0.876044
dbW.med^2	-0.05472	0.967096	0.032904
Night	0.37745	0	1

Model 3	Median Coeff.	Prob -	Prob +
Edge	0.025748	0.220254	0.779746
Open	-0.10532	0.945793	0.054208
D prod	-0.02243	0.688315	0.311685
D drill	-9.6E-05	0.495956	0.504044
D fac	0.244615	0.000268	0.999733
TR	0.000679	0.290155	0.709845
D rd	0.025445	0.27582	0.72418
dbW.med	0.00536	0.461314	0.538686
Night	0.376781	0	1

Model 4	Median Coeff.	Prob -	Prob +
Edge	0.024296	0.23062	0.76938
Open	-0.12141	0.966201	0.033799
D prod	-0.01619	0.635313	0.364688
D drill	0.007259	0.459126	0.540874
D fac	0.24575	5.75E-05	0.999943
TR	0.000719	0.278774	0.721226
D rd	0.023557	0.290991	0.709009
dbW.med	0.053858	0.215216	0.784784
dbW.med^2	-0.04827	0.945503	0.054498
Night	0.383386	0	1